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THE PROBABLE PHYSIOGNOMY OF THE CRETACEOUS PLANT POPULATION.

BY CONWAY MACMILLAN.

The sudden appearance of metaspermic plants in the rocks of the Cretaceous period has occasioned much discussion, and has always proved to be a *crux* to the writers on evolutional philosophy. Even in the latest work of authority on general evolutionary topics—*Darwin, and after Darwin*, by Romanes, the old and vague statements—concerning "probable breaks in the records," and possible remarkable accelerations of what are usually very slow processes,—may be found again, and have the air of being all that can yet be said with much show of reason from the evolutional point of view. The various opponents of Darwinism, and of evolution in its broader sense, have ever appealed to the sudden emergence of Cretaceous metaspermic plants as an unanswerable argument against the different development-hypotheses. There is not space here even to cite the numerous works in which the unexplained and sudden appearance of Cretaceous metaspermic plants has been adduced in condemnation of the various evolutionary hypotheses. All students who have kept pace with the controversial biological literature of the last thirty years, will readily recall the important part that the Cretaceous plants have played in the anti-evolution polemic.

In view of what has been stated above, the intent of this paper will be recognized as a sufficiently ambitious one, when it is stated to be an effort to show two facts, as developed by the study of modern plant-formations and the evidence of the fossils; first, that the appearance of Cretaceous metaspermic plants is proved, *by the fossils*, not to have been sudden, but gradual, and consequently, in Cretaceous time, the general preponderance of plant-population was strongly coniferous, fern and cycadean; and second, that the conditions of Cretaceous time were such that the new and scattered metaspermic plants were placed under circumstances similar to those in which to-day variation is most rapid and plasticity is greatest for each species and even for every individual.

The attempt to show that the high preponderance of metaspermic remains in the Cretaceous rocks is a sufficient proof of the high preponderance of pines, cycads, ferns and club-mosses in the Cretaceous forests is paradoxical enough to excite grave suspicions of the method by which such a result is reached, but the writer hopes to show that the absurdity of the statement is solely a superficial one, and that it is really capable of a defence both from experiment, observation and legitimate deduction. I have already presented in my recent work on the plants of the Minnesota valley the skeleton of the argument,[1] but desire here to amplify and extend the discussion, somewhat, to more fully cover the ground. If the conclusions that I have drawn are legitimate, and my knowledge of the literature of the subject sufficient to uphold my belief that certain new laws are determined, both of plant-distribution to-day and paleontological interpretation, it will be clear that the argument is an important one, and should be examined for what it may prove to be worth.

In the first place let us examine some of the observed facts of plant-distribution to-day. It is apparent that while species themselves are generally limited in some more or less definite manner and occupy a more or less considerable area of the earth's crust, there are several degrees of aggregation in which species play a subordinate part. We note the coniferous forest as distinct from the hardwood forest, the prairie knoll from the prairie swale, the mountain-side herbage and shrubbery from the herbage and shrubbery of the valley. The presence of these different zonal groups at different attitudes and latitudes was first pointed out in the modern way, by von Humboldt.[2] Since his time, the various groups of species, conditioned in some definite manner and, under climatic influences, acquiring characteristic habits or habitats, have been studied somewhat in detail. The great works of DeCandolle[3], Grisebach[4], Engler[5], Drude[6], and the numerous special brochures of these and of many other writers on geographical botany, have pointed out with much distinctness the existence of plant-formations. These formations are of different degrees. In the United States there are, in the eastern portion, two very distinct formations that belong to the highest division—namely, the forest and the prairie. These two great formations, in the broadest sense, are scarcely anywhere in contact with each other, but are separated by what may be a very narrow strip of plants imperfectly developed in either forest or prairie. The region occupied by such a transitional strip of plants I have named in the work cited above, a *tension-line.* Wherever two formations of different sorts, such as hardwood forest and coniferous forest, meadow and hillside-grassland, or any other two, come together, there is such a tension-line developed along the line of contact.

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[1] Metaspermæ of the Minnesota Valley, p. 602 (1892).

[2] Essai sur la Geographie des Plantes, suivi d'un Tableau Physique des Regions Equinoctiales.

De Distributione Geographica Plantarum, secundum cœli Temperium et altitudinem montium, Prolegomena.

The character of the tension-line between formations has received as yet very little study, and it is not possible to speak of it as exactly as one would wish. My own observations are confined to the tension-lines between forest and prairie in the Minnesota valley, a region of special study for the past two years. Certain interesting facts have been deduced. These may be noted as follows:

The plants of the tension-line consist of such species as are sparsely developed in the more central areas of the two adjacent formations, or in some cases of species very poorly developed in the solid parts of the two formations.

The number of individuals of the first group is generally greater over a given area along the tension-line than in the solid portions of the formations.

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[3] Gèographie Botanique Raisonnèe, on exposition des Faits Principaux et des Lois concernant la Distribution Geographique des Plantes de l'epoque actuelle. TOM. I, II (1855).

[4] La Vègètation du Globe, d'apres sa Disposition suivant les Climats, esquisse d'une Geographie Comparèe des Plantes, trad. par P. de Tchihatchef. TOM. I, II. (1877).

[5] Versuch einer Entwickelungsgeschichte der Pflanzenwelt, insbesondere der Florengebiete seit der Tertiärperiode. TH. I, II. (1879).

[6] Handbuch der Pflanzengeographie. (1890).

There is a tendency for plants of a higher phylogenetic type to accumulate in the tension-line area than characterizes either of the adjacent formations. Thus in the border of the wood and prairie one finds Asters, Helianthi, Solidagos, predominant over the lower Archichlamydeae or Monocotyledones.

There is a transition from typically prairie groups of grasses to the typical tension-line groups of species, and similarly from the typically forest groups of trees, in the hardwood belt.

The tension line is characterized by a greater comparative richness of species and luxuriance of individuals, in the matter of number, than the average of the adjacent formations.

The tension-line is not a fixed, but a moving line, and usually one formation or the other is in a condition of encroachment while its adjacent formation is in a condition of retreat.

The movement of the tension-line is felt some distance from the contact line of the two formations, so that, if forest is encroaching upon prairie, the characteristic composites of the tension-line are thrust out farther into the prairie.

From the interior regions of both adjacent formations plants "work out" into the tension-line area. Such plants are generally the imperfectly established.

The last point lends itself very easily to direct experiment. If a field of some well established perennial plant, as for instance, blue-grass (*Poa pratensis*) be selected, and several sunflower seeds, or thistle seeds, be planted in the center of it, it will happen that one or two plants of the composite species may reach maturity, and will then distribute seed outward in every direction. In three years time the composites will probably be ejected to the periphery of the field, and will have gained there a considerable foothold, while in the center of the field they will have gained but a slight foothold, and perhaps will not have retained what they had given them at first. A strong formation thus ejects to its periphery the plants that not in harmony with it, still strive to establish themselves. In the work cited above, I have termed this "the law of the ejection of the weaker." It may be seen operating in any wood or field, and is, I believe, one of the most important factors in the origin and modification of metaspermic species—although not generally recognized. It will be observed that while this ejection is purely biological, it nevertheless bears comparison with certain physical phenomena as when, for example, the water contained between the pores of adjacent solids is squeezed to the surface of the mass, and is thus ejected from its original, more central position.

It appears from the preceding analysis of conditions certainly existing and verifiable, that two adjacent formations do not actually come in contact, but are separated by the thicker or thinner band of tension-line species. It further appears that the tension-line group is made up of, and constantly replenished by plants ejected from the interiors of both formations, and reaching the tension-line as it were, to use a metaphor from chemical science, "in the nascent condition." This explains, or at least suggests the explanation of what otherwise would be difficult, viz., the large comparative number of species in the tension-line area, and the fact that higher types are aggregated there rather than in the solid portions of adjacent formations. For not only is the tension-area populated from the interiors of the adjacent formations, and thus comes to have a diversified group of inhabitants injected into it, but these inhabitants are likely to be the new forms, not in perfect harmony with the general mass of the formation in which they originated—and therefore they are ejected. Furthermore plants reach the tension-area "on the move"—their variations already begun and accentuated, it may be, by the forced journey to the periphery of the parent formation. Therefore both the actual numbers of species in the tension-area being great, and these species being derived from widely different habitat and environment conditions, together with the high degree of plasticity acquired in the ejection and after establishment in the tension-area, it becomes evident that it is precisely at such a contact-region between two formations that conditions are highly favorable for specific and generic and even ordinal variations to set in. Thus the increased number of species in the tension-area is seen to be in part the cause, and in part the result, of the high variability that is experimentally noted in such an area.

From the above, the explanation of the various peculiarities of the tension-line will readily be derived. Under the law of the struggle for existence, it will be seen that this struggle may be between individual and individual, individual and formation, and formation and formation. All three phases are developed at the tension-line and since the causes of evolution are working at their highest along this area, it happens that the results are numerically most apparent. The three phases of the struggle are not elsewhere so vividly brought to one's notice, for at least the third will be wanting or felt but indirectly. It appears, as a result of the examination, that the character of the tension-line, as made out by observation, is capable of illumination by experiment and of explanation by the general and well-known laws of evolution.

It is now my intention to show that the metaspermic plant-population of the Cretaceous, and especially of the Upper Cretaceous was a tension-line population. If this be possible, we shall expect that population to manifest tension-line characteristics.

In the first place it is necessary to gain some comprehension of the Cretaceous geography. I shall concern myself here only with the Upper Cretaceous of America. At the time of the deposition of the Cretaceous clays and sandstones, the North American continent was much more restricted than now. It extended little south of Illinois, and was cut by a great Mediterranean Sea into an eastern, larger and shorter, and a westtern, smaller and longer continent. The Mediterranean Sea extended from the south to the extreme north, and was doubtless highly saline in character. The coasts of this sea were generally low—at least this is derived from the evidence of the flora, according to Lesquereaux—but, here and there, doubtless varied by some rocky promontory or headland. The shores were marked by frequent bays and estuaries, and the rivers which flowed into the Cretaceous oceans were probably tide-streams to a marked degree. The general character of the country was low or morassic, but this was certainly broken by high uplifts, usually far inland. The coast-line of the ocean was therefore, so far as may be determined up to the present time, a generally low area, where vast stretches of sands or mud-flats were shifted about by the surf and by the inflowing waters of tributary streams. It is these sandy beaches and mud-flats that persist to-day as the Cretaceous rocks, bearing their countless imprints of archaic plants.

Considering next, for a moment, the character of the plant remains from the Cretaceous, we find that in the Lower Cretaceous, as studied by Fontaine, there are numerous ancient fern and cycadean types. These become less prominent in the Upper Cretaceous, so that in 1874, when, under the researches of Heer and Lesquereaux, already 130 species were described from the Dakota group, of these only five are ferns or cryptogamous plants, one doubtfully cycadean, six coniferous, two monocotyledonous, and the rest Dicotyledons—principally in the Archichlamydeæ, with only a very few (*Bicornes, Leguminosæ, Ebenaceæ,* etc.) referable to the Metachlamydeæ. The presence of the older types of cycads, conifers and ferns is important to be noted, for it is possible that the sole reason for their not appearing in countless numbers is the fact that they were cut off from the sandy-beaches and mud-flats by a thin but well-nigh continuous tension-line group of new and struggling Metaspermæ.

The study of shore-lines of modern seas is essential to the further working out of the hypothesis in process of development in this paper. The writer is not aware that observations have been made with the considerations in view that would make them useful either for support or objection. His own studies of sea-shore areas are confined to the observation of Cape Cod, Massachusetts, during a single month. While there he found that the older plants are more numerous in the inner regions, and the newer more numerous nearer the coast. The coast-line then seems to be a tension-area. While there are many pines on the Cape, these, so far as I could discover, were generally distributed inland, reaching the border of the sea only on high promontories, and on low lands being generally separated from it by strips of herbage, low shrubbery and hardwood timber. Further study of the sea-shore is needed along this line. But, apart from the testimony of the limited observation, it appears demonstrable that the coast-line, simply because it was peripheral, thus terminating ejections, must have developed a tension-line group of plants in Cretaceous times. That this tension-line was a relatively narrow one is proved by the great preponderance of metaspermic remains. For if it had been a broad one, the competition between older ferns and cycads, and newer metaspermic plants would doubtless have been sufficient to have brought down to the coast in larger numbers the more inland types of plants.

The picture of the Cretaceous plant physiognomy which these considerations brings before our eyes is of a great solid inland forest of conifers, cycads, ferns, and *Calamites* (?), bounded by a thin peripheral line of metaspermic trees, shrubs and herbs. This peripheral line extended up both sides of all estuaries, streams and rivers, and thus shut off the older, luxuriant and dominant flora from proper representation in the rocks of the period, as they have come down to us. An occasional inland plant was carried down some river and buried in the sands or shales at its mouth, and sometimes when the shores were high the inland types came close to the sea, and in the *Sequoias*, *Cunninghamites*, *Abietites*, *Zamieites* and other genera of the Cretaceous rocks, we derive a hint of the inland and general character of the plant population. The very fact, therefore, of the high metaspermic preponderance in the fossils—since it shows metaspermic plants to have been uniformly the coast population, and hence the tension-line population, is an argument in favor of supposing that metaspermic plants were actually very much less predominant in the general flora then than they were in Tertiary or Recent time.

Together with this disposition of the oft-repeated declaration that the Cretaceous Metaspermæ appeared with inexplicable suddenness, it will be seen that the other difficulty of their rapid and inordinate multiplication of species and genera is solved—so far as such notes constitute a solution. The tension-line position, with its tremendous increase of urgency to modify, and its concomitant increase of individual plasticity, explains the matter, so far as general explanations are of value. As the Metaspermæ began to fight their way back into the solid coniferous fern and cycadean forest, doubtless the same phenomena might have been noticed that are apparent to-day. The examination of a region where hardwood forest is encroaching upon coniferous is especially suggestive. The forerunners of the hardwood trees, various herbs and shrubs, insinuate themselves up the rivers and tributaries, closely followed by the trees themselves. In this way the coniferous plants and their numerous allies, the various heaths, cornels, club-mosses, etc., are isolated into phalanxes of smaller and smaller size. At last they become entirely surrounded by the invading types, and at the first opportunity are exterminated altogether. Without question similar scenes might have been noticed in the ancient Cretaceous forest when the tension-line group of plants waxed strong and began the backward march carried on through Tertiary time and resulting in the domination to-day of archichlamydeous trees in the extra-tropical forest regions, while metachlamydeous plants are in their turn characteristic of the tension-lines.

To summarize, in conclusion, what is at best a disconnected and imperfect attempt to contribute somewhat toward the analysis of a very difficult group of problems. A study of modern plant formations reveals the presence of tension-line areas in which higher types of plants may become aggregated, and where the general tendencies are toward a high degree of individual and specific variability. Such tension-lines are peripheral in position, and may be of different degrees of organization as they lie around formations of greater or less degree of integration. Newer types of plants are particularly likely to be forced into the tension-line habitat, under the law of the ejection of the weaker. Both observation and experiment show this. Such tension-lines doubtless characterized the Cretaceous formations as well as those of to-day. In them the weaker, because newer, types were aggregated, and in this way the littoral regions of the Cretaceous oceans came in all cases to be densely metaspermic in the character of their plant-population. The generally low elevation of the coasts contributed to this condition. The older types of plants, making up the bulk of the forest, were isolated from the shores and from the banks of streams, except very far inland. Consequently their remains are preserved only under exceptional conditions. That the metaspermic plants occupied the tension-line position indicates the preponderance of older types in the great inland stretches of country. The rapid appearance of new metaspermic types during the Cretaceous—and probably too in Jurassic time—was a result of the tension-line position into which they had been forced. The high development of the arboreal habit may be referred to similar causes.

The picture thus brought before the eyes differs much from the usual reconstructions of Cretaceous landscapes, but may be, nevertheless, a closer approximation to the truth. A final word may be added in regard to the conditions of the Triassic and even of earlier time. In those ages we may imagine the metaspermic types developing in the ancient forests of cycads —or even of *Lepidodendrons* and *Annularias*—and beginning their forced marches to the peripheral regions of the solid, archaic formations of their birth. Thus for century upon century they may have existed, and fail to appear in the fossils, because of their internal position in the formations. But when, after their long struggle for food and light and soil for support, they emerge upon the periphery of their parent formations we find them already arborescent or arboreal, and soon almost universal upon littoral areas. They then first come into a position where preservation in the rocks is possible.